

Nitrogen productivity of some conifers

GÖRAN I. ÅGREN

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Received August 20, 1982¹

Accepted January 18, 1983

ÅGREN, G. I. 1983. Nitrogen productivity of some conifers. Can. J. For. Res. **13**: 494–500.

Nitrogen productivity, expressed as annual yield of foliage per unit of nitrogen in the foliage, is recommended for interpreting responses to changes in nitrogen availability. This index can be directly coupled to growth and is well suited for application in mathematical analyses of tree or forest growth dynamics. This paper demonstrates that the nitrogen productivity decreases predictably as biomass increases probably as a result of the reduction in irradiance as the canopy becomes more dense. For five species of conifers from northern latitudes (*Picea abies* Karst., *Pseudotsuga menziesii* Mirb. Franco, *Pinus nigra* var. *maritima* (Ait.) Melv., *Pinus resinosa* Ait., and *Pinus sylvestris* L.) nitrogen productivity is shown to decrease linearly with increasing needle biomass. For a particular species, these regressions allow for estimation of maximum needle biomass.

ÅGREN, G. I. 1983. Nitrogen productivity of some conifers. Can. J. For. Res. **13**: 494–500.

Pour interpréter les réactions au changement de l'azote disponible, on propose la notion de productivité de l'azote, exprimée comme une production annuelle de feuillage par unité d'azote dans le feuillage. Cet indice peut être associé directement à la production et s'applique très bien à des analyses mathématiques de dynamique d'accroissement d'arbres ou de forêts. L'auteur montre que la productivité de l'azote décroît quand la biomasse s'accroît, probablement à cause de la réduction de rayonnement avec un couvert de plus en plus dense. Chez cinq essences résineuses des régions nordiques (*Picea abies* Karst., *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus nigra* var. *maritima* (Ait.) Melv., *Pinus resinosa* Ait. et *Pinus sylvestris* L.), la productivité de l'azote décroît de façon linéaire avec l'accroissement de la biomasse du feuillage. Pour une essence donnée, ces régressions permettent d'évaluer la biomasse maximale du feuillage.

[Traduit par le journal]

Introduction

Traditionally, studies of tree nutrition have focused upon changes in concentration of various nutrients in different tissues (cf. Morrison 1974). Nutrient concentrations, particularly of the foliage, have served as an index of the nutritional status of trees or stands. However, observed variations in nutrient concentrations have not been easily associated with production. One difficulty is that the same amount of nutrients can be allocated into variable amounts of foliage so that it might be better to express results as the product of concentration times tissue. This represents the "amount" of nutrient committed to growth of foliage. In this paper, I construct a framework for analysis, called "nitrogen productivity," based on this principle and relate it to growth.

I treat only nitrogen because it is commonly one of the most growth-limiting macronutrients and data are therefore readily available. I propose that the amount of biomass produced is directly related to the amount of nitrogen in that biomass through the nitrogen productivity. For field applications nitrogen productivity is best described as a collective property of a stand rather than for single trees. For simplicity, I restrict the analysis to the production of foliage, recognizing that the

growth of other tissue can be estimated from correlations with this variable (e.g., Ovington 1957; Whittaker and Woodwell 1968; Tamm 1974).

The approach is designed to provide a tool for analyses of rapidly changing growth of forests as well as other ecosystems. I therefore stress this objective. Other emphases might warrant, of course, other analyses.

Theory

Quite generally, the net increment in foliage may be described as the difference between production of new foliage and loss of old foliage. If the production rate is assumed proportional to the amount of nitrogen in the foliage (N) and the loss rate to the weight of foliage (W), the net increment in foliage can be written

$$[1] \quad dW/dt = P_{(N)} N - f W$$

Here, $P_{(N)}$ is the nitrogen productivity and f is the rate of tissue mortality. Both depend in principle not only upon biomass (W) and nitrogen (N) but also upon external variables such as weather and time (t). Equation 1 defines the nitrogen productivity as the amount of biomass produced per unit of nitrogen in that biomass per unit of time.

If we assume the rate of mortality (f) to be approximately constant, then, a constant nitrogen productivity ($P_{(N)}$) would allow the foliage to increase indefinitely

¹Revised manuscript received January 13, 1983.

with added amounts of nitrogen, an obvious impossibility. Hence, the nitrogen productivity should decrease as foliage biomass (W) increases. A decrease in the nitrogen productivity could result from internal shading, water stress, or increased respiration by nonphotosynthesizing tissue. Let us for simplicity assume that $P_{(N)}$ will decrease linearly. Hence,

$$[2] \quad P_{(N)} = a - bW$$

where a and b are species-specific parameters. Equations 1 and 2 imply that there is an upper limit to the amount of foliage, W_{\max} :

$$[3] \quad W_{\max} = \frac{a - f/(N/W)_{\max}}{b}$$

where $(N/W)_{\max}$ is the maximum optimal nitrogen concentration obtained without tissue injury (cf., Ingstad *et al.* 1981, Fig. 1). Equation 3 can be used for estimating the maximal leaf biomass of a forest once we have estimated the constituting parameters.

How much might self-shading account for the predicted reduction in the nitrogen productivity with increasing foliage biomass? In the Appendix, I present calculations demonstrating that simple application of Lambert–Beer's law to light penetration through foliage can fully account for the phenomenon. Derived from this exercise is an equation for canopy photosynthesis such that:

$$[4] \quad \frac{b}{a} \approx \frac{\gamma}{2(I_0/\alpha + 1)}$$

where γ is the light extinction coefficient (the fraction of light absorbed per unit of foliage penetrated), I_0 the light intensity above the canopy, and α the light intensity at which the photosynthetic rate is half that at saturation.

Results

Let us now apply these formulae to independent sets of data. I have chosen to select examples dealing with just foliage production to minimize confusion and calculations. The examples could easily be expanded to predict forest biomass accumulation. The foliage is well suited as a test tissue because, unlike the stem, it consists entirely of living tissue.

The data base available for evaluating the hypothesis, Eq. 2 only permits one comparison during a season, although the possibility exists of applying the equation to intervals over the growing season. In conifers with a relatively stable needle biomass it is possible to define an annual nitrogen productivity without concern for large within-year variations. For convenience, I define the nitrogen productivity from values at the end of the growing season: $P_{(N)} = (\text{current needle biomass})/(\text{total}$

nitrogen in all foliage). With deciduous species or with conifers with short-lived needles (e.g., *Pinus taeda*) this simple approach is not possible, and repeated samplings over the whole growing season would be required (Ingstad 1979a, 1980, 1981; Ericsson 1981a, 1981b).

Adequate data for testing the relationship formulated in Eq. 2 were available for *Picea abies* Karst. (Norway spruce), *Pseudotsuga menziesii* Mirb. Franco (Douglas-fir), and three species of *Pinus* (*P. nigra* var. *maritima* (Ait.) Melv. (Corsican pine), *P. resinosa* Ait. (Red pine), and *P. sylvestris* L. (Scots pine)) covering a wide range of ages, stand densities, soil conditions, and geographical locations (Table 1). Figure 1 displays graphically the relations, and statistical analyses are presented in Table 2. For *Picea abies* and *Pinus sylvestris* only are the data bases adequate (more than 20 samples) for statistical analysis. The other three species, however, appear to exhibit similar relationships. Although many other studies have been reported in the literature, most lack information on the necessary data (current needle biomass, total needle biomass, and the nitrogen pool in foliage).

Table 3 presents the results of the analysis of the effect of internal shading upon the nitrogen productivity. Jarvis *et al.* (1976) report values of 0.35–0.80 ha · ha⁻¹ for the light extinction coefficient (γ) for several coniferous species and under different light conditions. Data in Albrektson and Aronsson (1983), Miller and Miller (1976), and Ovington (1957) indicate that 1 kg of Scots pine needles have a projected area of around $3 \cdot 10^{-4}$ ha, whereas Nihlgård (1972) gives $6.4 \cdot 10^{-4}$ kg dry weight ha⁻¹ for Norway spruce, thus giving values of γ between 10^{-4} and $5 \cdot 10^{-4}$ kg dry weight ha⁻¹. For further analysis γ was assumed to be $3 \cdot 10^{-4}$ kg dry weight ha⁻¹. An important question is which value should be chosen for I_0 , the light intensity above the canopy. In Table 3, $I_0 = 400 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ corresponding to an average value over the growing season is used (Linder and Lohammar 1981). With these values, good agreement between the two sides of Eq. 4 is obtained. From this analysis I therefore draw the conclusion that the main factor responsible for the decrease in nitrogen productivity with increasing needle biomass is the increasing internal shading within the canopy.

From the same data as used for Fig. 1 it is also possible to get an estimate of the mortality rate of the foliage by assuming it equal to the ratio of current to total needle biomass. This is correct if the needle biomass is in equilibrium with the environment (ceiling LAI) but results in an overestimate of the mortality rate if canopy biomass or leaf area index are still increasing. Actually, surprisingly little variation in the rate of needle mortality in relation to total needle biomass was

TABLE 1. Data about stands used in the analysis

Species	Number of stands*	Ages (years)	Stand densities (trees/ha)	Location	Reference	Code†
<i>Picea abies</i>	8	23	2900–3900	Southern Sweden	Tamm (1968, 1975)	A
<i>Picea abies</i>	10	15	1625–3025	Central Sweden	Tamm (1974)	B
<i>Picea abies</i>	1	55	880	Southern Sweden	Nihlgård (1972)	C
<i>Picea abies</i>	1	200	356	Arkhangelsk	Marchenko and Karlov (1962)	D
<i>Picea abies</i>	1	70	1332	Czechoslovakia	Klimo (1980)	E
<i>Picea abies</i>	3	34–115	nr	Solling	Cole and Rapp (1981)	F
<i>Pseudotsuga menziesii</i>	3	22–450	nr	Washington State	Cole and Rapp (1981)	A
<i>Pseudotsuga menziesii</i>	1	nr‡	nr	Washington State	Gessel <i>et al.</i> (1973)	B
<i>Pseudotsuga menziesii</i>	1	15–20	16000	British Columbia	Webber (1977)	C
<i>Pinus nigra</i>	5	36	2110	England	Miller and Miller (1976)	A
					Miller <i>et al.</i> (1976)	
<i>Pinus resinosa</i>	4	40	2103–2638	New York State	Wittwer <i>et al.</i> (1975)	A
<i>Pinus resinosa</i>	2	32	3460	New York State	Fornes <i>et al.</i> (1970)	B
<i>Pinus sylvestris</i>	5	25	1131–1280	Central Sweden	Albrektson and Aronsson (1983)	A
<i>Pinus sylvestris</i>	9	7–55	760–5640	England	Ovington (1957, 1959)	B
<i>Pinus sylvestris</i>	3	28, 45, 47	2911, 1420, 845	Southern Finland	Mälkönen (1974)	C
<i>Pinus sylvestris</i>	1	120	393	Central Sweden	Bringmark (1977)	D
<i>Pinus sylvestris</i>	1	64	815	Scotland	Wright and Will (1958)	E
<i>Pinus sylvestris</i>	19	20	1095	Central Sweden	Own data	F

*Can also be number of different plots or treatments within an experiment.

†The code refers to the symbols used in Fig. 1.

‡Not reported.

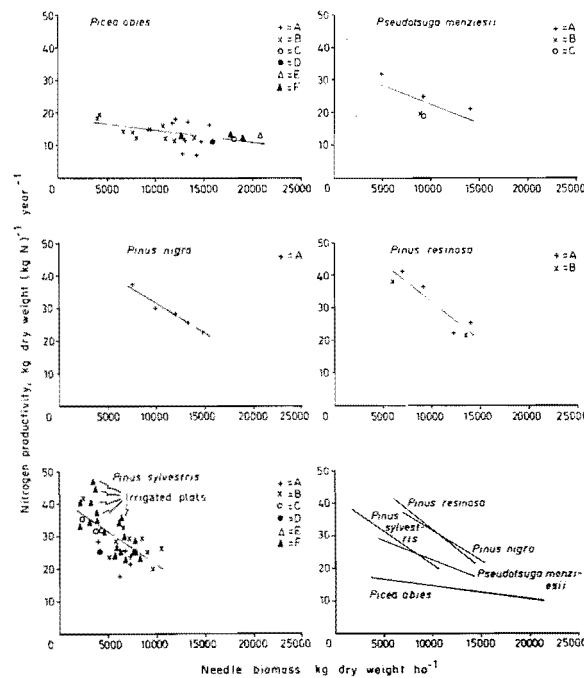


FIG. 1. Representations of the relations between nitrogen productivity and needle biomass. Different data sets are represented with different symbols, references are given in Table 1. The regressions for equations in Table 2 are also given. These regression lines are combined for comparison in the lower right-hand subpicture. The length of the regression lines there indicate the variability in the needle biomasses in the underlying data sets.

observed, but to get a definite value I chose the upper end of the regression of mortality rate on total needle biomass.

Ingestad (1979b) found that the optimal nitrogen concentration of *Picea abies* and *Pinus sylvestris* both lie close to 2% of dry weight. Assuming this to be true for the other coniferous species (although van den Burg (1971) gives higher values for *Pinus nigra* and *Pseudotsuga menziesii*) the maximal needle biomasses were calculated from Eq. 3 and are presented in Table 4. These values correspond quite well with the highest values of needle biomass reported in the literature.

Discussion

Although the data base was small, results indicate a general pattern. The three pine species from the northern temperate zone all exhibited similar regression equations (Fig. 1). The spruce, on the other hand, was different, having much lower nitrogen productivity ($P_{(N)}$) but also showing very little reduction in nitrogen productivity with increasing needle biomass. The latter should be expected because spruce is a shade-tolerant species and grows satisfactorily under low light. The Douglas-fir falls between these two. The two parameters a and b are strongly correlated ($p = 0.952$, $P < 5\%$), suggesting that coniferous species may have evolved either to be highly efficient at high light intensities or to be moderately efficient at a wide range of light intensities.

Precisions of the regressions presented, Table 2, are

TABLE 2. Regressions of nitrogen productivity ($a - bW$) on needle biomass (W) for different species

Species	Parameters with 95% confidence intervals				
	a^*	b^\dagger	$S_{y \cdot x}$	r^2	n
<i>Picea abies</i>	18.4 ± 3.8	$0.000\ 377 \pm 0.000\ 288$	2.92	0.251	24
<i>Pseudotsuga menziesii</i>	34.4 ± 22.1	$0.001\ 17 \pm 0.002\ 24$	4.55	0.480	5
<i>Pinus nigra</i>	50.2 ± 8.8	$0.001\ 84 \pm 0.000\ 75$	1.38	0.953	5
<i>Pinus resinosa</i>	55.7 ± 14.1	$0.002\ 41 \pm 0.001\ 30$	3.64	0.869	6
<i>Pinus sylvestris</i>	41.4 ± 4.5	$0.002\ 04 \pm 0.000\ 74$	4.98	0.465	38

*Kilograms of dry weight per kilogram of nitrogen per year.

†Hectares per kilogram of nitrogen per year.

TABLE 3. Numerical evaluation of Eq. 4

Species	$\alpha \mu E \cdot m^{-2} \cdot s^{-1}$	γ		Reference for α
		$2(I_0/\alpha + 1)$	b/a^*	
<i>Picea abies</i>	98	29.5×10^{-6}	20.5×10^{-6}	Fuchs <i>et al.</i> (1977)
<i>Pseudotsuga menziesii</i>	258	58.8×10^{-6}	34.0×10^{-6}	Künstle (1971)
<i>Pinus nigra</i>	178	46.2×10^{-6}	36.7×10^{-6}	van den Driessche and Wareing (1966)
<i>Pinus resinosa</i>	189	48.1×10^{-6}	43.3×10^{-6}	Bourdeau and Laverick (1958)
<i>Pinus sylvestris</i>	330	67.8×10^{-6}	49.3×10^{-6}	Troeng and Linder (1982)

*Calculated from Table 2.

TABLE 4. Maximal needle biomasses

Species	Loss rate (year ⁻¹)	Maximal needle biomass (kg dry weight · ha ⁻¹)		Minimal nitrogen concentration*
		From Eq. 3	Observed	
<i>Picea abies</i>	0.15	28 300	20 600	0.82
<i>Pseudotsuga menziesii</i>	0.17	22 000	14 100	0.49
<i>Pinus nigra</i>	0.43	15 500	14 800	0.86
<i>Pinus resinosa</i>	0.23	18 400	14 100	0.41
<i>Pinus sylvestris</i>	0.39	10 700	10 500	0.94

*Percentage of dry weight. This is the lowest nitrogen concentration that allows growth according to Eq. 1.

not remarkable, but it must be remembered that the data sets represent stands from a variety of sites. Looking in some detail at the data, Fig. 1, one suspects that the nitrogen productivity of Scots pine in Scandinavia (data sets A, C, D, and F) is lower than in Britain (data sets B and E), which could be a result of longer periods of photosynthetic activity in Britain. However, the differences are not statistically significant.

The data set A for Norway spruce and Scots pine are taken from fertilizer trials. In these data sets there are three points (two for the spruce and one for the pine) falling well below the regression lines. These points correspond to the highest level of fertilizer applications, applications that probably were super-optimal. On the other hand, it is possible that improved availability of water might increase the nitrogen productivity as indicated by the position of the irrigated plots from data set E for Scots pine.

In this paper I have assumed that the nitrogen productivity can be treated as independent of nitrogen concentration. From laboratory studies (Ingsted 1979a, 1980, 1981) we know that this is not so. At low nitrogen concentrations the nitrogen productivity decreases. However, as nitrogen concentrations increase, the nitrogen productivity increases rapidly up to a constant level. Thus, over wide ranges of nitrogen concentrations the nitrogen productivity may, indeed, be regarded as constant. In situations where the nitrogen concentrations fall to very low levels, as might be the case in other ecosystems like grasslands, reformulations are necessary, not in the idea as such but in its interpretation, Eq. 2.

The formulation of the nitrogen productivity ($P_{(N)}$) can be given a form that is easily interpretable biologically and also mathematically tractable, Eq. 2. Therefore, the simple Eq. 1 becomes a well-formulated model, providing us with a convenient tool for analysing tree and forest growth both under natural conditions and under influence of perturbations (Ingsted *et al.* 1981; Ågren 1983a, 1983b). Simplicity in formulations and interpretations have been the major criteria in this paper. I want to stress this objective because

other objectives could have implied other interpretations of the basic data (cf. Ågren 1981). In particular, there is often a conflict between accuracy of quantitative prediction and qualitative understanding, where the former may require the inclusion of several details obscuring the transparency of the problem to the detriment of the latter.

Leaf and Madgwick (1960) suggested that to "properly interpret analytical data it is necessary to convert results from concentrations to contents on an areal basis." The nitrogen productivity provides a tool for doing this and warrants further testing in predicting forest growth. The approach also appears promising for comparing species and interpreting their ecological differences. Studies on other nutrients and environmental factors may also justify testing within the general framework presented for assessing nitrogen constraints upon forest growth.

Acknowledgement

I want to thank F. Andersson, B. Axelsson, F. Berendse, E. Bosatta, T. Fagerström, and T. Ingsted for valuable criticism of the manuscript. R. Waring added much to the logic and language of the final version of the manuscript. This work was supported by the Swedish Natural Science Research Council.

- ÅGREN, G. I. 1981. Problems involved in modelling tree growth. In *Understanding and predicting tree growth*. Edited by S. Linder. Stud. For. Suec. **160**: 7–18.
- . 1983a. Model analysis of some consequences of acid precipitation on forest growth. In *Ecological effects of acid deposition*, National Swedish Environment Protection Board Report. PM 1636: 233–244.
- . 1983b. Model analysis of some stability properties of northern coniferous forests. Lesovedenie. In press.
- ALBREKTSON, A., and A. ARONSSON. 1983. Growth, structure, biomass and mineral nutrient contents of a young Scots pine stand after several years of fertilization. Swedish Univ. Agric. Sci. Dep. Ecol. Environ. Res. In press.
- BOURDEAU, P. F., and M. L. LAVERICK. 1958. Tolerance and photosynthetic adaptability to light intensity in white

- pine, red pine, hemlock and Ailanthus seedlings. *For. Sci.* **4**: 196–207.
- BRINGMARK, L. 1977. A bioelement budget of an old Scots pine forest in Central Sweden. *Silva Fenn.* **11**: 201–209.
- COLE, D. W., and M. RAPP. 1981. Elemental cycling in forest ecosystems. In *Dynamic properties of forest ecosystems* (International Biological Programme 23). Edited by D. E. Reichle. Cambridge University Press, Cambridge.
- ERICSSON, T. 1981a. Effects of varied nitrogen stress on growth and nutrition of *Salix*. *Physiol. Plant.* **51**: 423–429.
- 1981b. Effects of varied nutrient stress on growth and nutrition of *Salix* cuttings grown in low conductivity solutions. *Physiol. Plant.* **52**: 239–244.
- FORNES, R. H., J. V. BERGLUND, and A. L. LEAF. 1970. A comparison of the growth and nutrition of *Picea abies* (L.) Karst. and *Pinus resinosa* Ait. on a K-deficient site subjected to K fertilization. *Plant Soil*, **33**: 345–360.
- FUCHS, M., E.-D. SCHULZE, and M. I. FUCHS. 1977. Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. II. Climatic control of carbon dioxide uptake. *Oecologia*, **29**: 329–340.
- GESSEL, S. P., D. W. COLE, and E. C. STEINBRENNER. 1973. Nitrogen balances in forest ecosystems of Pacific Northwest. *Soil Biol. Biochem.* **5**: 19–34.
- INGESTAD, T. 1979a. Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. *Physiol. Plant.* **45**: 149–157.
- 1979b. Mineral nutrient requirements of *Pinus sylvestris* and *Picea abies* seedlings. *Physiol. Plant.* **45**: 373–380.
- 1980. Growth, nutrition and nitrogen fixation in grey alder at varied rate of nitrogen addition. *Physiol. Plant.* **50**: 353–364.
- 1981. Nutrition and growth of birch and grey alder seedlings in low conductivity solutions and at varied relative rates of nutrient addition. *Physiol. Plant.* **52**: 454–466.
- INGESTAD, T., A. ARONSSON, and G. I. ÅGREN. 1981. Nutrient flux density model of mineral nutrition in conifer ecosystems. In *Understanding and predicting tree growth*. Edited by S. Linder. *Stud. For. Suec.* **160**: 61–72.
- JARVIS, P. G., G. B. JAMES, and J. J. LANDSBERG. 1976. Coniferous forest. In *Vegetation and the atmosphere*. Vol. 2. Case studies. Edited by J. L. Monteith. Academic Press, London, New York, San Francisco.
- KLIMO, E. 1980. Nutrient cycling within the ecosystem of a man-made spruce forest. In *Stability of Spruce Forest Ecosystems*. International Symposium, Brno 1979. Edited by E. Klimo. University of Agriculture, Brno, Czechoslovakia.
- KÜNSTLE, E. 1971. Der Jahresgang des CO₂-Gaswechsels von einjährigen Douglasientrieben in einem 20-jährigen Bestand. *Allg. Forst-Jagdztg.* **142**: 105–108.
- LEAF, A. L., and H. A. I. MADGWICK. 1960. Evaluation of chemical analyses of soils and plants as aids in intensive soil management. *Proc. World For. Congr. 5th*, **1**: 554–557.
- LINDER, S., and T. LOHAMMAR. 1981. Amount and quality of information on CO₂-exchange required for estimating annual carbon balance of coniferous trees. In *Understanding and predicting tree growth*. Edited by S. Linder. *Stud. For. Suec.* **160**: 73–87.
- MÄLKÖNEN, E. 1974. Annual primary production and nutrient cycle in some Scots pine stands. *Commun. Inst. For. Fenn.* **84.5**: 1–87.
- MARCHENKO, A. I., and E. M. KARLOV. 1962. Mineralnii obmen v elovix lecax cevernoi taigi i lecotyndri arxangelckoi oblacti. *Pochvovednie*, **7**: 52–66.
- MILLER, H. G., and J. D. MILLER. 1976. Effect of nitrogen supply on net primary production in Corsican pine. *J. Appl. Ecol.* **13**: 249–256.
- MILLER, H. G., J. D. MILLER, and O. J. L. PAULINE. 1976. Effect of nitrogen supply on nutrient uptake in Corsican pine. *J. Appl. Ecol.* **13**: 955–966.
- MORRISON, K. I. 1974. Mineral nutrition of conifers with special reference to nutrient status interpretation: a review of the literature. *Can. For. Serv. Inf. Rep. No.* 1343.
- NIHLGÅRD, B. 1972. Plant biomass, primary production and distribution of chemical elements in a beech and planted spruce forest. *Oikos*, **23**: 69–81.
- OVINGTON, J. D. 1957. Dry-matter production by *Pinus sylvestris* (L.). *Ann. Bot. (London)*, **21**: 287–314.
- 1959. Mineral content of plantations of *Pinus sylvestris* (L.). *Ann. Bot. (London)*, **23**: 75–88.
- TAMM, C. O. 1968. An attempt to assess the optimum nitrogen level in Norway spruce under field conditions. *Stud. For. Suec.* **61**: 1–67.
- 1974. Experiments to analyse the behaviour of a young spruce forest at different nutrient levels. *Proceedings of the First International Congress of Ecology*, September 8–14, The Hague, The Netherlands. pp. 266–272.
- 1975. Plant nutrients as limiting factors in ecosystem dynamics. *Proceedings of a symposium*. (V. General Assembly, IBP). National Academy of Sciences, Washington, D.C. pp. 123–132.
- TROENG, E., and S. LINDER. 1982. Gas exchange in a 20-year-old stand of Scots pine. II. Variation in net photosynthesis and transpiration within and between trees. *Physiol. Plant.* **54**: 15–23.
- VAN DEN BURG, J. 1971. Some experiments in the mineral nutrition of forest tree seedlings. (Report of a study at the Royal College of Forestry, Stockholm.) Forest Research Station "De Dorschamp", Wageningen, Netherlands. *Int. Rep. No.* 8. pp. 1–67.
- VAN DEN DRIESSCHE, R., and P. F. WAREING. 1966. Dry-matter production and photosynthesis in pine seedlings. *Ann. Bot. (London)*, **30**: 673–682.
- WEBBER, B. D. 1977. Biomass and nutrient distribution patterns in a young *Pseudotsuga menziesii* ecosystem. *Can. J. For. Res.* **7**: 326–334.
- WITTWER, R. F., A. L. LEAF, and D. H. BICKELHAUPT. 1975. Biomass and chemical composition of fertilized and (or) irrigated *Pinus resinosa* Ait. plantations. *Plant Soil*, **42**: 629–651.
- WHITTAKER, R. H., and G. M. WOODWELL. 1968. Dimension and production relations of trees and shrubs in the Brookhaven forest, New York. *J. Ecol.* **56**: 1–25.
- WRIGHT, T. W., and G. M. WILL. 1958. The nutrient content of Scots and Corsican pines growing on sand dunes. *Forestry*, **31**: 13–25.

Appendix

Derivation of Eq. 4

Assume that the light response of the photosynthetic rate can be described by

$$[1A] \quad P(I) = P_m \frac{I}{I + \alpha}$$

for the whole canopy, where I is light intensity, P_m is the photosynthetic rate per unit needle biomass at light saturation and α a parameter. Let $\rho(z)$ be the needle biomass density at depth z in the canopy ($W = \int_0^L dz \rho(z)$), and let further the light extinction in the canopy be described by Lambert-Beer's law

$$[2A] \quad I(z) = I_0 \exp \left\{ -\gamma \int_0^z \rho(z') dz' \right\}$$

where I_0 is the light intensity above the canopy and γ a parameter. The photosynthetic rate of the whole canopy, $P_{tot}(W)$, can now be calculated

$$[3A] \quad P_{tot} = \int_0^L dz P_m \frac{I(z)}{I(z) + \alpha} = \frac{P_m}{\gamma} \ln \frac{I_0 + \alpha}{I_0 \exp \{-\gamma W\} + \alpha}$$

Equation 3A is an equation for the instantaneous rate of photosynthesis in the whole canopy. In order to connect P_{tot} with the nitrogen productivity, I_0 and P_m will be treated as constants. Then, P_{tot} is also equal to the average photosynthetic

rate. It is reasonable to expect that as photosynthetic rate goes up at constant nitrogen content, the ratio between the amounts of photosynthate and nitrogen increases. This should lead to an increase in nitrogen productivity. I express this relationship by assuming that the nitrogen productivity is proportional to the photosynthetic rate per unit needle biomass, i.e., $P_{tot}(W) = k P_{(N)}(W)$, where k is the proportionality constant. Dividing both sides with their respective value at $W = 0$ removes the proportionality constant, yielding

$$[4A] \quad \frac{a - bW}{a} \approx \frac{P_{tot}(W)/W}{P_{tot}(0)/0} = \frac{P_m I_0}{I_0 + \alpha}$$

It is clear that Eq. 4A is not an exact relationship because the right-hand side is not a linear function of W . However, for the present purpose and within the range of W that is relevant in this context, the right-hand side of Eq. 4A is approximated as a linear function. From the construction of Eq. 4A it is clear that the two sides are equal at $W = 0$. I estimate the slope of the right-hand side with its slope at $W = 0$, which gives

$$[5A] \quad \frac{b}{a} \approx \frac{\gamma}{2(I_0/\alpha + 1)}$$

This is the relationship between b/a and the photosynthesis related parameters I_0 , α , and γ that should hold if the decrease in nitrogen productivity could entirely be attributed to internal shading.